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Five *Nolanea* spp. nov. from Brazil

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Abstract—Five new species of *Nolanea* (*Entolomataceae*, *Agaricales*)—*N. albertinae*, *N. atropapillata*, *N. pallidosalmonea*, *N. parvispora,* and *N. tricholomatoidea*—were collected from the São Paulo metropolitan region. Phylogenetic analyses based on partial sequences of the mitochondrial small subunit (mtSSU), nuclear large subunit (nLSU) and second largest RNA polymerase subunit (rpb2), confirm that all these species belong to *Nolanea*. Morphological descriptions, comments, illustrations, scanning electron microscopy and color photos are included.

Key words—basidiomycetes, *Entoloma*, Neotropical fungi, South America, taxonomy

Introduction

Currently, *Nolanea* has two main circumscriptions, one according to Largent (1994) and Henkel & al. (2014) as *Nolanea* (Fr.) P. Kumm., and the other according to Noordeloos (1992, 2004) and Noordeloos & Gates (2012) as *Entoloma* subg. *Nolanea* (Fr.) Noordel. Both circumscriptions agree that *Nolanea* comprises species often mycenoid with the pileus surface typically hygrophanous, usually translucent-striate and with angled basidiospores with five, six or seven angles in profile view, which can be subisodiametric or heterodiametric. The main difference between the accepted circumscriptions of the genus *Nolanea* is in the pileipellis structure. Largent (1994) considers *Nolanea* to encompass only species that have a pileipellis composed of two layers, with a suprapellis composed of a cutis or a repent entangled hyphae

layer overlying a subpellis of inflated hyphae, whereas Noordeloos accepts species in *Entoloma* subg. *Nolanea* in which the repent, cylindrical hyphae of the pileipellis often (but not necessarily always) overlie a distinct differentiated subpellis of inflated cells.

In general, the few phylogenetic studies that include *Nolanea* species do not define which circumscription is the most appropriate for the group; additionally, they suggest *Nolanea* can be polyphyletic (Co-David & al. 2009, Baroni & Matheny 2011). However, *Nolanea* species are always in the Nolanea–Claudopus clade, independent of the combination of loci used: mtSSU, nLSU, and rpb2 (Co-David & al. 2009, Baroni & Matheny 2011) or ITS, nLSU, and rpb2 (Kinoshita & al. 2012). Also, it is usually possible to visualize two separate branches within the Nolanea–Claudopus clade, with a clade of *Nolanea* species separate from a clade comprising *Claudopus* species.

More recent molecular studies of *Entoloma* subg. *Nolanea* (Vila & al. 2013, Raj & al. 2014, Raj & Manimohan 2016) examined *Nolanea* species using only ITS sequences, with special emphasis on taxa delimitation and new taxa proposition. The phylogeny produced in these studies supports, even with only ITS sequences, the recognition of *Nolanea* as a good phylogenetic group and would seem to support *Nolanea* as an autonomous genus in the *Entolomataceae*.

Nolanea (with about 250 names in MycoBank and Index Fungorum) is considered a common and speciose genus, especially in temperate regions (Noordeloos 1992, 2004, Largent 1994, Horak 2008), but it is also present in tropical and subtropical regions (Romagnesi & Giles 1979). In Brazil of the 23 *Nolanea* species recorded (Rick 1919, 1920, 1930, 1961, Bresadola 1920, Singer 1953, Horak 1977, Capelari 1989, Putzke & Cavalcanti 1997, Pegler 1997, de Meijer 2001, 2006, Rosa 2002), eleven have been cited and/or described by Rick (1919, 1920, 1930, 1961, Singer 1953) and are considered as incertae sedis (Horak 1977). Many other species have been reported in dissertations (Capelari 1989, Rosa 2002), an identification key (Pegler 1997), and lists (Singer 1953, de Meijer 2001, 2006), but only three have been published with a full description (Putzke & Cavalcanti 1997).

In this work, we describe five new species found in the São Paulo metropolitan region accompanied by molecular information and phylogenetic analyses.

Materials & methods

Basidiomata collection and morphological observations

The studied materials were collected mainly at the Parque Estadual da Cantareira and the Parque Estadual das Fontes do Ipiranga in São Paulo City and Reserva

Table I. Collections used in the phylogenetic analyses

Cl. = Claudopus; E. = Entoloma; I. = Inocephalus; L. = Leptonia; P. = Pouzarella; Rh. = Rhodocybe; R. = Richoniella; T. = Trichopilus; Sequences generated in this study in **bold.**

NCBI species name	GenBank acc. no.			Voucher	Origin
	RPB2	LSU	mtSSU		
Cl. minutoincanus	HQ731517	HQ731514	HQ731511	DLL 9871	Australia, NSW
Cl. viscosus	HQ731518	HQ731516	HQ731513	DLL 9788	Australia, QLD
E. abortivum	GU384642	GU384616	GU384595	TB6693	USA, NY
	GQ289222	GQ289150	GQ289290	den Bakker 92	Canada
E. albidoquadratum	GQ289223	GQ289151	GQ289291	Manimohan 667-**T**	India, KL
E. bloxamii	GQ289226	GQ289154	GQ289294	Noordeloos 200442	Austria
E. cephalotrichum	GQ289229	GQ289157	GQ289297	Ulje 1997-08-01	Netherlands
E. conferendum	GQ289231	GQ289160	GQ289300	Noordeloos 200313	Belgium
E. cf. *conferendum*	—	JQ320115	—	HKAS 48953	China, SC
E. gasteromycetoides	GQ289235	GQ289164	GQ289304	Gates E2031	Australia, TAS
E. haastii	GQ289238	GQ289167	GQ289307	Noordeloos 2004055	Australia, TAS
E. hebes	GQ289241	GQ289170	GQ289310	Hartman 1992-10-28	Netherlands
E. nidorosum	GU384643	GU384617	GU384596	TB9971	USA, NY
E. pallideradicatum	GQ289247	GQ289176	GQ289316	Hausknecht	Austria
E. parasiticum	GQ289248	GQ289177	GQ289317	Noordeloos 200330	Belgium
E. porphyrescens	GQ289253	GQ289182	GQ289322	Noordeloos 2004113	Australia, TAS
E. procerum	GQ289254	GQ289183	GQ289323	Noordeloos 2004070	Australia, TAS
E. pygmaeopapillatum	GQ289256	GQ289185	GQ289325	Noordeloos 200364	Slovakia
Entoloma readiae	GQ289257	GQ289186	GQ289326	Noordeloos 2004050	Australia, TAS
E. sericatum	GQ289260	GQ289189	GQ289329	Noordeloos 200328	Slovakia
E. sericionitidum	EF421016	AF261315	EF421098	TB7144	USA, NY
E. serrulatum	GQ289263	GQ289192	GQ289332	Noordeloos 2004062	Australia, TAS
E. sinuatum	GQ289264	GQ289193	GQ289333	Wisman 2003-09-19	Netherlands
E. strictius	—	AF042620	—	M96/10	—
E. strictius var. *isabellinus*	GU384641	GU384618	GU384594	TB7710	USA, TN
E. turbidum	GU384656	GU384630	GU384603	TB6949	USA, NY
E. undatum	GQ289270	GQ289202	GQ289342	Noordeloos 200327	Belgium

NCBI species name	GenBank acc. no.			Voucher	Origin
	RPB2	LSU	mtSSU		
E. valdeumbonatum	GQ289271	GQ289203	GQ289343	Meusers E4565 [T]	Germany
I. murrayi	GU384637	GU384620	GU384590	VHAs02.02	—
I. sp. MCA2479	GU384640	GU384622	GU384593	MCA2479	—
L. serrulata	GU384634	GU384624	GU384588	VHAs01.02	—
L. sp. MCA1486	GU384635	GU384623	GU384589	MCA1486	—
N. albertinae	—	**KF738937**	**KF738925**	FK1731	Brazil, RJ
	KF771345	**KF738938**	**KF738926**	FK1732	Brazil, RJ
	KF771344	**KF738936**	**KF738924**	FK0935-**T**	Brazil, SP
N. atropapillata	—	**KF738940**	**KF738929**	FK0898-**T**	Brazil, SP
N. cetrata	**KF771346**	**KF738942**	**KF738927**	DLL9531	USA, CA
	—	AF261319	—	TB7382	USA, NY
N. conferenda	**KF771351**	**KF738946**	**KF738935**	11CA014	USA, CA
N. conferenda	—	AF261321	—	TB7660	USA, NY
N. hirtipes	—	AF261320	—	K1171992	
N. pallidosalmonea	—	**KF738941**	**KF738930**	FK0891	Brazil, SP
N. parvispora	**KF771348**	**KF738943**	**KF738931**	FK1140	Brazil, SC
	—	—	**KF738932**	FK2135	Brazil, SC
N. sericea	DQ367435	DQ367423	EF421099	VHAs 03/02	—
	GQ289262	GQ289191	GQ289331	Noordeloos 200329	Slovakia
	KF771349	**KF738944**	**KF738933**	11CA055	USA, CA
	KF771350	**KF738945**	**KF738934**	11CA056	USA, CA
	—	AF261318	—	TB6506	USA, CA
N. strictior	EF421017	—	EF421100	DUKE-JM96/10	
N. tricholomatoidea	**KF771347**	**KF738939**	**KF738928**	FK1049-**T**	Brazil, SP
P. albostrigosa	HQ876513	HQ876535	HQ876557	Largent 9641	Australia
P. lasia	HQ876507	HQ876529	HQ876555	Largent 9662	Australia
P. nodospora	—	AF261308	—	TB5716	USA, SC
P. setiformis	HQ876503	HQ876525	HQ876525	Largent 9809	Australia
Rhodocybe trachyspora	GU384658	GU384629	GU384605	TB5856	USA, CA
Richoniella asterospora	JF706311	JF706310	—	PBM3268	USA, TN
Trichopilus porphyrophaeus	—	AF261290	—	TB6957	USA, NC
Outgroup					
Clitocybe dealbata	DQ825407	AF223175	AF357138	IE-BSG-HC95cp3	—
Lyophyllum leucophaeatum	DQ367434	AF223202	AF357101	IE-BSG-HAe251.97	—

Biológica de Paranapiacaba in Santo André City, in remnants of the Atlantic Forest in São Paulo State, Southeast Brazil.

Revived sections of tissues from dried basidiomata mounted in 5% KOH, 5% NH_4OH, or 1% aqueous Congo Red dye used to stain hyaline structures were examined microscopically. All the micrographs were drawn with the aid of a drawing tube. 'Q' represents the minimum and maximum length/width quotient, and 'Qm' represents the mean length/width quotient of the total sample of measured spores. The pileipellis structure was examined from the middle portion of the pileus and not the disc or margin. The specimens were deposited in the herbarium of the Instituto de Botânica (SP) and of the Royal Botanic Gardens (K). The samples were prepared for SEM following Baroni (1981) and scanning electron micrographs (SEMs) were made using a LEO 435 VP scanning electron microscope.

DNA extraction, amplification, sequence analyses

The DNA was extracted with hexadecyltrimethylammonium bromide (CTAB) (Ferreira & Grattapaglia 1995) using lyophilized tissues from basidiomata ground to a fine power in liquid nitrogen. The sample was resuspended in 50 µL of TE and stored at –20 °C. The partial sequences of the mitochondrial small subunit (mtSSU) were amplified via the polymerase chain reaction (PCR) primed by MS1 and MS2 (White & al. 1990); the 28S nuclear large subunit (nLSU) rDNA was amplified using LR0R and LR5 (Moncalvo & al. 2000); the ITS1-5.8S-ITS2 was amplified using ITS1-F and ITS4 (White & al. 1990, Gardes & Bruns 1993); and the second largest subunit of the RNA Polymerase II (rpb*2*) using rpb*2*-i6F and rpb2-i7R (Co-David & al. 2009) or rpb2-F1 and rpb2-R1b (Largent & al. 2013). The PCRs were performed in 25–50 µL reaction volumes, where the reaction concentration was 1× for PCR Buffer, 2 mM for MgCl2, 0.2 mM for each dNTP, 0.5 µM for each forward and reverse primer, and 0.025 U of Taq polymerase. Products from multiple reactions were pooled for weak PCR amplifications. The reaction was performed using the following cycling parameters: 94 °C for 2 min, 34 cycles at 94 °C for 45 s, 50 °C (54C° for rpb2) for 1 min and 10 s and 72 °C for 2 min, and then 72 °C for 10 min. PCR amplifications products were purified using the AxyPrep PCR Clean-up Kit (Axygen Biosciences, Union City, USA) or alternatively, using the ExoSapIT kit following the protocols outlined in Largent & al. (2011). DNA sequencing reactions were performed with BigDye Terminator v3.1 Cycle Sequencing Kit. The sequences were run in a ThermoFisher 3730 DNA Analyzer using Sequencing Analysis 5.3.1 and Base Caller KB. The forward and reverse sequences for each sample were aligned and edited using CodonCode Aligner or Sequencher.

The phylogenetic analysis was conducted using sequences obtained in this study and sequences found in GenBank of species traditionally accepted as *Nolanea* [Nolanea–Claudopus clade sensu Co-David & al. (2009) and Baroni & Matheny (2011)] (Table I). *Lyophyllum leucophaeatum* (P. Karst.) P. Karst. and *Clitocybe dealbata* (Sowerby) P. Kummer were selected as outgroups based on phylogenetic analyses performed by Co-David & al. (2009). The sequences were manually aligned using Se-Al Sequence Alignment Editor; spliceosomal introns in the rpb2

were delimited using Augustus ver. 2.4 webserver (Stanke & al. 2008) and omitted along with ambiguous sites in mtSSU. For these phylogenetic analyses, sequences from the three genes including missing data were assembled. The final alignment after the exclusion of introns and ambiguous sites was 3162 bp including gaps: 592 bp for the mtSSU, 1390 bp for the nLSU and 1180 bp for the rpb2 (Tree-BASE database ID14850).

Phylogenetic analyses were performed using maximum likelihood (ML), Bayesian Inference (BI), and maximum parsimony (MP). For the BI, the best-fit model of nucleotide substitution was performed using the Akaike information criterion (AIC) in TOPALI v.2 (Milne & al. 2009). ML analysis was performed using RAxML 7.0.4 with a GTR + G model according to recommendations (Stamatakis 2006, Stamatakis & al. 2008). Support for nodes was tested using 1000 bootstrap replicates. For the BI phylogeny, the best-fit model of nucleotide substitution for each gene partition and codon for the rpb2 (GTR + G for LSU, mtSSU and codons and 3 of rpb2, and GTR + G + I for first codon of rpb2). The BI was performed with MrBayes 3.2.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) specifying four chains (one cold, three heated) for 2,000,000 generations (sampling trees every 1000 generations), with a burn-in of 30,000 generations. MP heuristic searches were performed using the program TNT (Goloboff 1999, Nixon 1999, Goloboff & al. 2008). Tree searches were conducted with equal weights and treating gaps as a fifth character state. Branch support was calculated with 1000 bootstrap replicates. A bootstrap value of 70% was considered significant for ML and MP. The Bayesian posterior probability (BPP) statistical support values of branches were considered informative if ≥ 0.95.

Phylogenetic results

The DNA sequences obtained, including partial sequences of the nLSU, mtSSU, and rpb2m are summarized in Table I. Additionally, sequences obtained from *Nolanea albertinae* (FK0912: KF679349, FK0935 [holotype]: KF679348), *N. atropapillata* (FK0898 [holotype]: KF679354), *N. pallidosalmonea* (FK0891 [holotype]: KF738923), *N. parvispora* (FK1140 [holotype]: KF679353) and *N. tricholomatoidea* (FK1049 [holotype]: KF679352) were deposited in GenBank.

The phylogenetic analyses placed all five species studied into /Nolanea–Claudopus (Co-David & al. 2009, Baroni & Matheny 2011, Kinoshita & al. 2012), an unsupported clade based on ML, MP, and BPP. The phylogenies place all five species into one of two strongly supported internal clades (Fig. 1) in the /Nolanea clade with other species of *Nolanea*.

Taxonomy

Five new species are described and illustrated with line drawings, macroscopic photographs and SEMs of basidiospores.

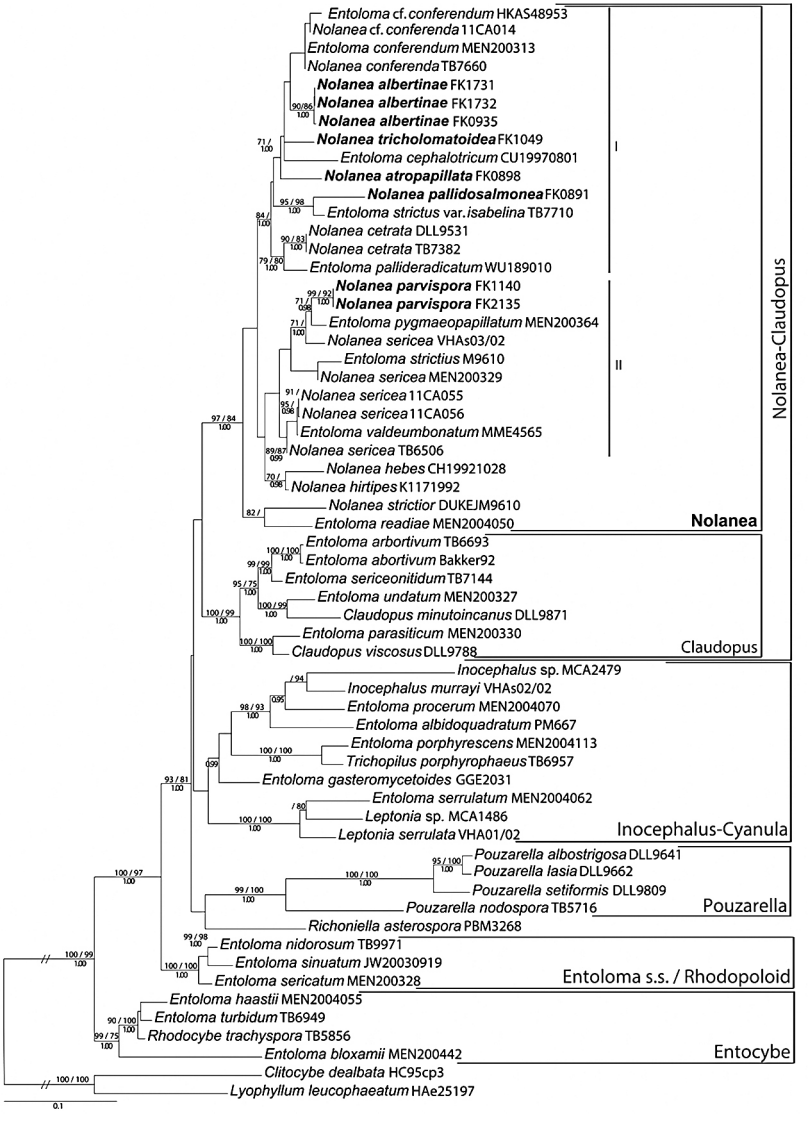

Fig. 1. Phylogram of maximum likelihood (ML) phylogenetic reconstruction using rpb2, nLSU, and mtSSU sequences. Support is indicated with ML/MP bootstrap percentage above and Bayesian posterior probabilities (BPP) below branches. The names of species studied in this paper are in **boldface.** I. Species with heterodiametric basidiospores. II. Species with iso- to subisodiametric basidiospores.

Nolanea albertinae Karstedt & Capelari, **sp. nov.** FIGS. 2A–E, 3, 8A,B

MB826784

Differs from *Entoloma belouvense* by its smaller basidiospores and presence of refractive hyphae.

TYPE—Brazil, São Paulo State, Santo André: Reserva Biológica de Paranapiacaba, 23°46′S 46°18′W, trail 15, 18.V.2006, F. Karstedt & M. Capelari FK0935 (**Holotype**: SP; GenBank KF771344, KF738936, KF738924).

ETYMOLOGY—an honour to Albertina Teresinha Karstedt.

PILEUS 14–18 mm diam., broadly conic, conico-convex, convex, plano-convex or plane, often slightly papillate, rarely with the center plane or depressed, pale brown, brown, dark brown (chocolate-colored), or gray-brown, center often darker than the margin, surface glabrous or with a few appressed, concolorous radial fibrils, when humid strongly translucent-striate, when dry, opaque, hygrophanous, margin slightly or strongly eroded. PILEUS CONTEXT very thin, whitish. LAMELLAE adnexed or sinuate, pale pinkish brown, subdistant, with 1–5 lamellulae (3 series), margin slightly eroded. STIPE 36–71 × 1–4 mm, often cylindrical, rarely tapered above or subbulbous over base, brownish beige, pale brown, gray-brown or ocher brown, rarely yellowish brown or concolorous with pileus, apex always paler than the base, sometimes beige or whitish, surface glabrous, often with the apex slightly pruinose, fibrillose-twisted, hollow, base of stipe often with a white tomentum. SPORE PRINT not recorded.

BASIDIOSPORES 7.5–10(–11.2) × 5–7.5 µm (Q = 1.16–1.75, Qm = 1.36), heterodiametric, strongly angled, with 5 or 6 angles in profile, slightly pinkish brown, thin-walled. BASIDIA 23–37 × 8.7–15 µm, clavate, hyaline, thin-walled, tetrasporic. LAMELLAE EDGES heterogeneous. CHEILOCYSTIDIA always present, dispersed or present [in portion of] on the lamellae edges near the stipe, 26–68 × 5–7.5 µm, cylindrical, often apex capitate, hyaline, thin-walled. PLEUROCYSTIDIA absent. LAMELLAR TRAMA subparallel, with hyphae 5–40 µm diam., cylindrical or fusiform, hyaline, thin-walled; subhymenium ramose. PILEITRAMA composed of radially arranged and parallel hyphae, with hyphae 8.7–25 µm diam., inflated or fusiform, hyaline, thin-walled. PILEIPELLIS a cutis, made up of cylindrical hyphae, with brown intracellular pigment, hyphae thin-walled, 3.7–7.5 µm diam., with cylindrical or cylindrical-clavate terminal elements; subpellis made up of inflated or fusiform, hyaline, thin-walled hyphae, 10–37 µm diam. STIPITIPELLIS a cutis of straw yellow, thin-walled hyphae 5–15 µm diam. CAULOCYSTIDIA absent. CLAMP CONNECTIONS present, but inconspicuous. REFRACTIVE HYPHAE present at pileipellis.

Fig. 2. Basidiomata. ***Nolanea albertinae***: a. FK735; b. FK883; c. FK912; d. FK935 (holotype); e. FK1111. ***N. atropapillata***: f. FK649; g. FK898 (holotype). ***N. pallidosalmonea***: h. (FK892, holotype). ***N. parvispora***: i. FK664 (holotype); j. FK689; k. FK794. ***N. tricholomatoidea***: l. (FK1049, holotype). Scale bars = 1 cm. Photos: a, b, d–j, l: F. Karstedt; c, k: M. Capelari.

Habitat—Solitary or sometimes gregarious, on litter or in soil with fragmented organic material.

Additional specimens examined—**BRAZIL, São Paulo State: São Paulo**, Parque Estadual da Cantareira, Núcleo Engordador, 23°20′S 46°41′W, Macuco trail, 27.IV.2006, F. Karstedt & M. Capelari FK630 (SP); 29.VI.2006, F. Karstedt & M. Capelari FK0690 (SP); 19.IX.2006, F. Karstedt & M. Capelari FK0735 (SP); Cachoeira trail, 20.III.2007, F. Karstedt & al. FK0883 (SP); 29.V.2007, F. Karstedt & al. FK0912 (SP); 13.III.2008, F. Karstedt FK1101 (SP); Parque Estadual das Fontes do Ipiranga, 23°39′S 46°37′W, Nascente trail, 20.VI.2006, F. Karstedt & al. FK0682 (SP); 28.VIII.2008, F. Karstedt & K. Patekoski FK1111 (SP); Santo André, Reserva Biológica de Paranapiacaba, 23°46′S 46°18′W, trail 15, 18.V.2006, F. Karstedt & M. Capelari FK0651 (SP), FK0652 (SP); trail 2, 18.V.2006, F. Karstedt & M. Capelari FK0656 (SP); trail 3, 22.VI.2006, F. Karstedt FK0685 (SP); trail 1, 23.VIII.2006, F. Karstedt FK0727

(SP). **Santa Catarina State:** Gaspar, #1111 Pedro Schmitt Street, hill behind the João Pedro Lenfers' house, 02.VIII.2008, F. Karstedt & A.T. Karstedt FK1110 (SP). Rio de Janeiro State: Parque Nacional do Itatiaia, 11.I.2011, F. Karstedt, P.B. Schwartsburd & J.B. Pereira FK1731 (SP; GenBank KF738937, KF738925), FK1732 (SP; GenBank KF771345, KF738938, KF738926).

Comments—*Nolanea albertinae* apparently is a common species in the Atlantic Forest of southern and southeastern Brazil; additionally it is usually solitary and almost undetectable in the litter, considering that both have similar color. *Nolanea albertinae* is similar to *N. atripes* Dennis and *N. pseudopapillata* Pegler, which are both described from Central America (Horak 1977, Pegler 1983). It also resembles *Entoloma dissimile* (Singer) E. Horak (described from Argentina; Singer 1969, Horak 1977), *N. fuscifolia* (Peck) Sacc. (described from the United States (Peck 1874, Hesler 1963) but also found in Argentina; Singer 1969) and *Entoloma novum* E. Horak, (described from Chile; Horak 1977). These species have a similar stature including the mycenoid habit; a pileus that is brownish, conical to plane, papillate and hygrophanous; a similar pileipellis with brown pigmented repent hyphae; and similarly shaped and sized basidiospores, 7–10 × 5–7.5 µm. All also can be separated morphologically besides lacking the cylindrical to capitate cheilocystidia that characterize *N. albertinae*.

Nolanea atripes has a darker pileus, no cheilocystidia, and pileipellis with a vacuolar pigment (Pegler 1983). *Nolanea pseudopapillata*, *Entoloma dissimile* and *Entoloma novum* differ (from *N. albertinae*) by the absence of cheilocystidia and clamp connections and by the presence of encrusted pileipellis hyphae (Singer 1969, Horak 1977, Pegler 1983). *Nolanea fuscifolia* grows on wood (instead soil or litter), has a dark brown pileus, lacks cheilocystidia, and has clamp connections; additionally, *N. fuscifolia* was originally described from New York (Peck 1874, Hesler 1963). *Nolanea fuscifolia* sensu Singer (1969) from Argentina, is closer to *Nolanea albertinae* in its very infrequent cheilocystidia and not (or only slightly) encrusted pigmentation; however it is distinguished by its growth on dead wood and by the presence of fusoid-ventricose caulocystidia.

The species most closely related to *Nolanea albertinae* is *Entoloma belouvense* Noordel. & Hauskn. from the Republic of Seychelles, an island archipelago in the Indian Ocean off the east coast of Africa (Noordeloos & Hausknecht 2007). *Entoloma belouvense* has similar macroscopic features and scattered cheilocystidia that are cylindrical and often capitate. However, in addition to its different distribution, *N. albertinae* has distinctly smaller basidiospores (7.5–10 × 5–7.5 µm versus 10-12 x 6-7,5 µm) and the presence of refractive hyphae at pileipellis.

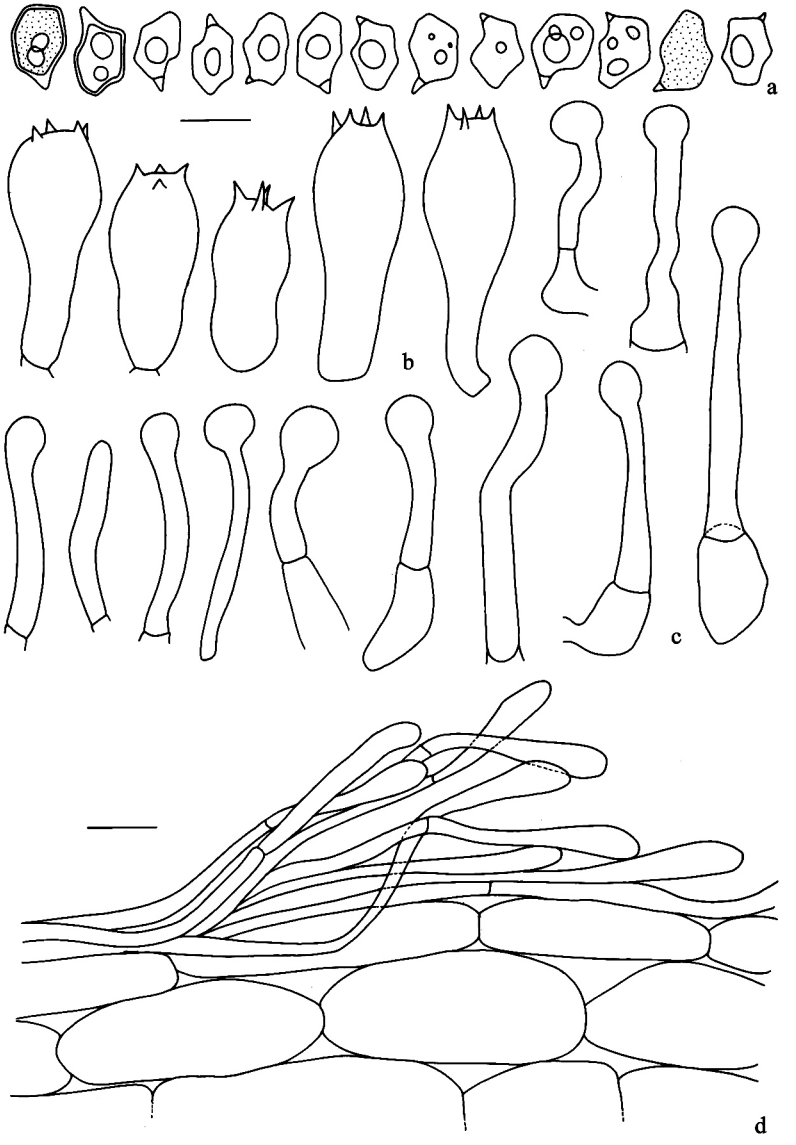

Fig. 3. *Nolanea albertinae* (holotype, FK935):
a. Basidiospores; b. Basidia; c. Cheilocystidia; d. Pileipellis.
Scale bars: a–c = 10 μm; d = 20 μm.

Nolanea atropapillata Karstedt & Capelari, **sp. nov.** FIGS. 2F,G, 4, 8C,D

MB805603

Differs from *N. albertinae, N. atripes, N. pseudopapillata*, and *Entoloma dissimile* by its bisporic basidia, by its intracellular and encrusted pigment in pileipellis hyphae, and by the absence of clamp connections.

TYPE—Brazil, São Paulo State, Santo André: Reserva Biológica de Paranapiacaba, 23°46′S 46°18′W, Estrada Frederico Carlos Hoehne, 12.IV.2007, F. Karstedt & al. FK0898 (**Holotype**: SP, GenBank KF738940, KF738929).

ETYMOLOGY—refers to the color of the papillae that are darker than the pileus.

PILEUS 9–25 mm diam., convex, plano-convex or plane, papillate or umbonate, brown or dark brown, darker in the center compared to the edge, turning grayish brown or pale gray-brown with blackish papilla, surface smooth or sometimes slightly squamulose-fibrillose at center, striate-translucent, strongly hygrophanous then silky, margin slightly eroded or split and upturned with age. PILEUS CONTEXT very thin. LAMELLAE almost free, narrowly adnexed, pink or pink-brown, subdistant, with 1–5 lamellulae (2 tiers), margin smooth or slightly eroded. STIPE 20–55 × 1–7 mm, cylindrical, with subbulbous base or slightly tapering upwards from swollen base, nearly white, pale beige or very pale brown, apex that is paler than the base, fibrillose-twisted, hollow, base of stipe often with a white tomentum. SPORE PRINT not recorded.

BASIDIOSPORES 8.7–12.5 × 6.2–8.7 µm (Q = 1.16–1.6, Qm = 1.4), heterodiametric, strongly angled, with 5–6 angles in profile, slightly brownish pink, thin-walled. BASIDIA 20–35 × 7.5–10 µm, clavate, hyaline, thin-walled, bisporic. LAMELLAE EDGE fertile. CHEILOCYSTIDIA and PLEUROCYSTIDIA absent. LAMELLAR TRAMA made up of regular cylindrical or fusiform, hyaline, thin-walled hyphae, 6.2–26 µm diam.; subhymenium ramose. PILEITRAMA composed of radially arranged and parallel cylindrical or fusiform, hyaline, thin-walled hyphae, 3.7–37 µm diam. PILEIPELLIS a cutis, suprapellis made up of cylindrical hyphae, with brown intracellular pigment, sometimes with brown encrusted pigment, hyphae thick or thin-walled, 2.5–18 µm diam.; terminal elements repent or anticlinal and then almost a trichoderm, cylindrical or cylindrical-clavate at center of pileus; subpellis composed of inflated or fusiform, hyaline or slightly straw yellow, thin-walled hyphae, 13.7–44 µm diam. STIPITIPELLIS a cutis made up of hyaline or slightly straw yellow, thin-walled hyphae, 2.5–10 µm diam. CAULOCYSTIDIA absent. CLAMP CONNECTIONS absent. REFRACTIVE HYPHAE not observed.

HABITAT—Solitary or dispersed in litter.

ADDITIONAL SPECIMENS EXAMINED—**BRAZIL, SÃO PAULO STATE, Santo André**: Reserva Biológica de Paranapiacaba, 23°46′S 46°18′W, trail 12, 18.V.2006, F. Karstedt

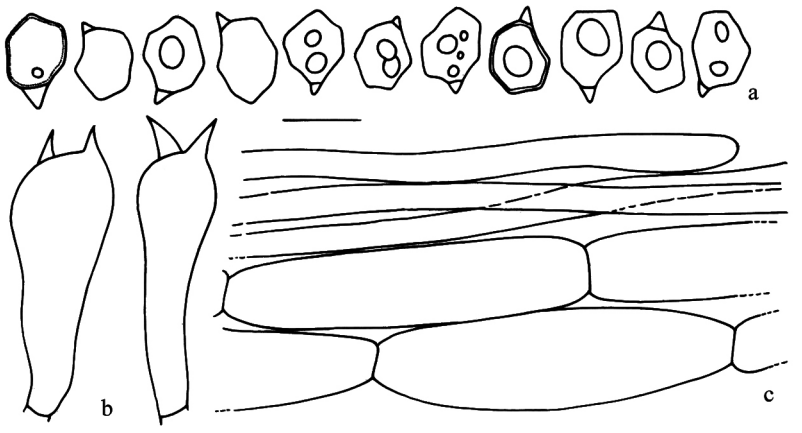

Fig. 4. *Nolanea atropapillata* (holotype, FK898): a. Basidiospores; b. Basidia; c. Pileipellis. Scale bars: a, b = 10 μm; c = 20 μm.

& M. Capelari FK0649 (SP), FK0650 (SP); trail 6, 18.V.2006, F. Karstedt & M. Capelari FK0655 (SP); Estrada Frederico Carlos Hoehne, 12.V.2007, F. Karstedt & al. FK0899 (SP).

Comments—*Nolanea atropapillata* resembles *N. albertinae*, *N. atripes*, *N. pseudopapillata*, and *Entoloma dissimile* from South America and *N. fuscifolia* from the United States. All of these species have papillate, pale brown pilei with a darker center and a translucent-striate surface and heterodiametric basidiospores in the 8–13 × 6–9 μm range. However, all differ from *N. atropapillata* in producing tetrasporic basidia and clamp connections. *Nolanea atripes* is further distinguished by its slender basidioma, membranaceous pileus, and black stipe (Dennis 1961). The description of *N. atripes* by Pegler (1983) differs from the Dennis's type description, in which Dennis (1961) emphasized the contrast between the black stipe and gray-brown pileus, while Pegler (1983) described the stipe as pale brown to dark, and the basidiomata illustrated is much more robust.

Nolanea albertinae also differs by the presence of cheilocystidia and absence of encrustations in the pileipellis hyphae, and *Entoloma dissimile* differs by the pileipellis as a cutis without a differentiated subpellis. *Nolanea fuscifolia* is distinguished by its subnodulose basidiospores (Hesler 1963, Singer 1969) and *N. pseudopapillata* by its strongly heterodiametric basidiospores (Q = 1.61, Pegler 1983).

Nolanea pallidosalmonea Karstedt & Capelari, **sp. nov.** FIGS. 2H, 5, 8E,F

MB805604

Nolanea pallidosalmonea differs from other *Nolanea* spp. by its delicate and slender basidiomata, by a pale pinkish salmon pileus with salmon pink striations and slightly brownish center, by 5–6-angled heterodiametric basidiospores, by a pileipellis composed of repent hyphae, and by the presence of refractive hyphae.

TYPE—Brazil, São Paulo State, Santo André: Reserva Biológica de Paranapiacaba, 23°46′S 46°18′W, trail 1, 23.III.2007, F. Karstedt & al. FK0892 (**Holotype**, SP; **isotype** K).

ETYMOLOGY—the name refers to the pale salmon pink coloration of the basidioma.

PILEUS 4–15 mm diam., convex, slightly papillate, when young with more pronounced papillae, very pale salmon pink or whitish salmon pink, darker at the center and strongly translucent-striate when in fresh condition, hygrophanous and then whitish from the margin towards the center and finally whitish salmon pink and when dry, sometimes slightly brownish at center, translucent-striate, after opaque and silky-fibrillose, margin entire. PILEUS CONTEXT thin, translucent. LAMELLAE adnexed or sinuate, pale pink, ventricose, subdistant, with 2 tiers of lamellulae. STIPE 25–54 × 1–3 mm, cylindrical or slightly tapering, pale salmon pink or light brownish, hollow, fibrous, with a small amount of white tomentum at the base. SPORE PRINT not recorded.

BASIDIOSPORES 8.7–10 × 6.2–7.5 µm (Q = 1.16–1.6; Qm = 1.41), heterodiametric, strongly angled, with (5)6–7 angles in profile view, hyaline or slightly pinkish brown, thin-walled. BASIDIA 25–37 × 8.7–11.2 µm, clavate, hyaline, thin-walled, tetrasporic. PLEUROCYSTIDIA and CHEILOCYSTIDIA absent. LAMELLAE EDGE fertile. LAMELLAR TRAMA subparallel, hyphae with 5–20 µm diam., cylindrical or slightly inflated, sometimes fusiform, hyaline, thin-walled; subhymenium ramose. PILEITRAMA trama composed of regular cylindrical, inflated or fusiform, hyaline, thin-walled hyphae, 11.2–26 µm diam. PILEIPELLIS a cutis made up of cylindrical, hyaline, thin-walled hyphae, 2.5–8.7 µm diam.; subpellis made up of inflated or fusiform, hyaline, thin-walled hyphae, 10–21 µm diam. STIPITIPELLIS a cutis of hyaline, thin-walled hyphae, 3.7–12.5 µm diam. CAULOCYSTIDIA not observed. CLAMP CONNECTIONS absent. REFRACTIVE HYPHAE abundant in pileipellis.

HABITAT— Gregarious or scattered, on soil.

ADDITIONAL SPECIMEN EXAMINED—**BRAZIL**, **SÃO PAULO STATE**, **Santo André**: Reserva Biológica de Paranapiacaba, 23°46′S 46°18′W, trail 1, 23.III.2007, F. Karstedt & al. FK0891 (SP; GenBank KF738941, KF738930).

COMMENTS—*Nolanea pallidosalmonea* resembles *Entoloma quadratum* (Berk. & M.A. Curtis) E. Horak, cited from Borneo, Singapore, Costa Rica, United

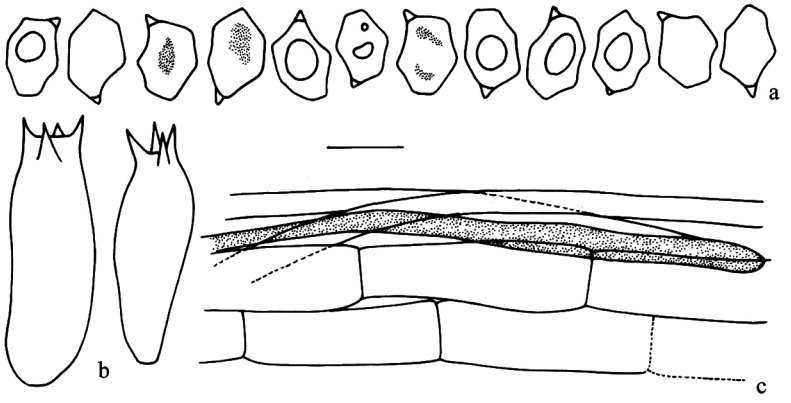

Fig. 5. *Nolanea pallidosalmonea* (holotype, FK892): a. Basidiospores; b. Basidia; c. Pileipellis. Scale bars: a, b = 10 μm; c = 20 μm.

States, Madagascar, Malaysia and Papua New Guinea, in its conical pileus and a smooth surface (a cutis) that is salmon colored. However, *E. quadratum* is clearly separated from *N. pallidosalmonea* by its cuboidal basidiospores and clavate cheilocystidia (Horak 1975, 1977, Baroni & Halling 2000).

Nolanea minuta P. Karst., described from Europe, is another species with pale and pinkish basidiomata, a silky-fibrillose pileus surface, heterodiametric basidiospores, and absence of cheilocystidia. However, *N. minuta* differs from *N. pallidosalmonea* in basidiospores with 5–7 angles in profile view, and a pileitrama composed of hyphae with intracellular and encrusted pigments (Noordeloos 1980).

Nolanea parvispora Karstedt & Capelari, **sp. nov.** Figs. 2I–K, 6, 8G–I

MB805605

Nolanea parvispora differs from other *Nolanea* spp. by its lignicolous habitat, pale beige pileus with dark center, stipe with a dark base and pale apex, sinuate lamellae, small (6.2–7.5 × 6.2–7.5 μm) isodiametric basidiospores, a lack of cystidia, and a pileipellis composed of repent hyphae with dispersed groups of anticlinal hyphae.

Type—Brazil, São Paulo State, Santo André: Parque Estadual da Cantareira, 23°20′S 46°41′W, Núcleo Engordador, Cachoeira trail, 25.V.2006, F. Karstedt & M. Capelari FK0664 (**Holotype**, SP).

Etymology—refers to the small size of the basidiospores.

Pileus 13–23 mm diam., convex, plano-convex or plane, sometimes with a slightly or prominent papilla or slightly depressed at the center, whitish beige

or pale brownish beige or light pinkish beige, brown at the center (insertion of stipe), smooth and sometimes pruinose at the center, glabrous, translucent-striate, margin revolute, even, or sometimes lobate. Pileus context very thin. Lamellae sinuate, white or pinkish beige, abundant, with 5–7 lamellulae (2 series), margin even. Stipe 25–42 × 2–4 cm, cylindrical or flattened, brown or brownish translucent, beige at the apex, surface smooth, base with white tomentum. Spore print pinkish. Basidiospores 6.2–7.5 × 6.2–7.5 µm (Q = 1–1.2; Qm = 1.1), isodiametric, with 5–6 angles in profile view, slightly pinkish, thin-walled. Basidia 27–43 × 8.7–10 µm, clavate, hyaline, thin-walled, tetrasporic. Pleurocystidia and cheilocystidia absent. Lamellae edge fertile. Lamellar trama subregular, cylindrical, inflated or fusiform, hyaline, thin-walled hyphae 3.7–12.5 µm diam.; subhymenium ramose. Pileitrama regular, made up of cylindrical, inflated or fusiform, hyaline, thin-walled hyphae, 3.7–25 µm diam. Pileipellis a cutis composed of cylindrical, hyaline or pale straw yellow, thin-walled hyphae, 6.2–13.7 µm diam., with dispersed or clustered thin-walled cylindrical or clavate, hyaline or pale straw yellow anticlinal terminal elements; subpellis made up of inflated or fusiform, hyaline, thin-walled hyphae 10–20 µm diam. Stipitipellis a cutis, made up of hyaline or pale straw yellow, sometimes with encrusted (external) yellow-brown pigment, thin or thick-walled hyphae, 6.2–16.2 µm diam. Caulocystidia rare, cylindrical, clavate or ventricose, with pale straw yellow plasmatic pigment, thin-walled, 28–75 × 2.5–7.5 µm. Clamp connections absent. Refractive hyphae present in pileipellis.

Habitat—Solitary or gregarious, on hardwood.

Additional specimens examined—**BRAZIL, São Paulo State, São Paulo**: Parque Estadual da Cantareira, Núcleo Engordador, 23°20′S 46°41′W, Macuco trail, 29.VI.2006, F. Karstedt & M. Capelari FK689 (SP); Cachoeira trail, 29.VI.2006, F. Karstedt & M. Capelari FK0696 (SP); 25.VII.2006, F. Karstedt & M. Capelari FK0723 (SP); 24.X.2006, F. Karstedt & M. Capelari FK794 (SP); 30.X.2007, F. Karstedt & al. FK0926 (SP). **Santa Catarina State**, Joinville: Reserva Particular de Patrimônio Natural Caetezal, 02.II.2009, F. Karstedt FK1140 (SP; GenBank KF771348, KF738943, KF738931); Corupá, Reserva Particular de Patrimônio Natural Emíleo F. Battistella, falls route, 12.XII.2011, F. Karstedt FK2135 (FLOR; GenBank KF738932).

Comments—*Rhodophyllus avellanicolor* Romagn. & Gilles, *Nolanea mazophora* (Berk. & Broome) Pegler, *Entoloma myceliosum* E. Horak, and *Entoloma imbecille* (E. Horak) E. Horak ex Segedin & Pennycook [≡ *E. fragile* E. Horak, nom. illegit.] are among the few species that resemble *Nolanea parvispora* based on pale basidiomata and isodiametric basidiospores measuring c. 7 × 7 µm. *Rhodophyllus avellanicolor*, described from Africa, and

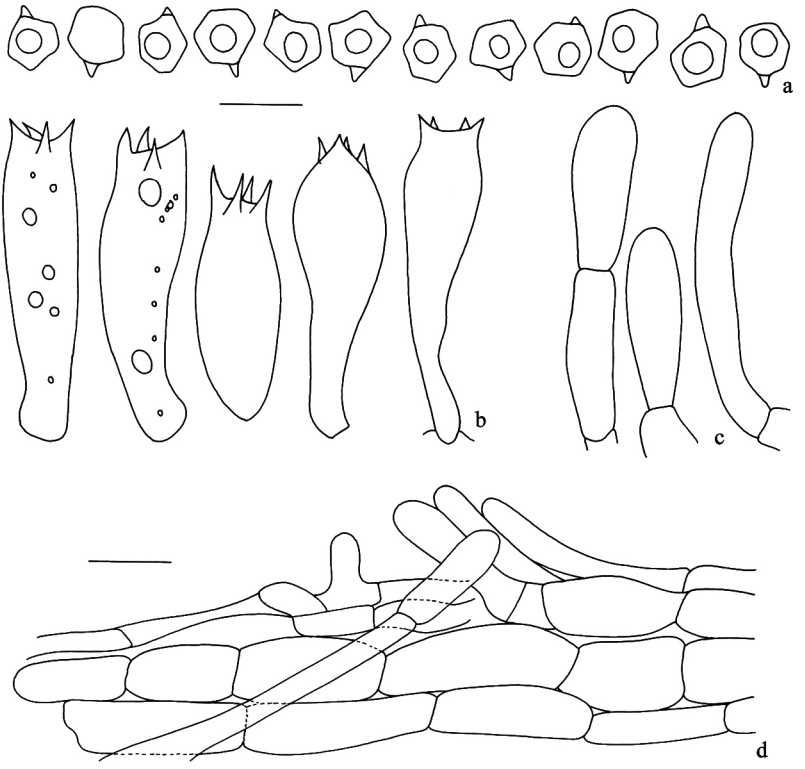

Fig. 6. *Nolanea parvispora* (holotype, FK664):
a. Basidiospores; b. Basidia; c. Caulocystidia; d. Pileipellis.
Scale bars: a–c = 10 μm; d = 20 μm.

Nolanea mazophora, described from Sri Lanka, are terrestrial. *Rhodophyllus avellanicolor* has clamp connections (Romagnesi & Gilles 1979) and *N. mazophora* has a convex pileus with prominent papillae (Pegler 1977, Horak 1980).

Entoloma myceliosum, described from Chile, is also lignicolous but differs from *N. parvispora* by having a white pileus and stipe and a pileus surface densely covered by white fibrils (Horak 1977). *Entoloma imbecille,* found in New Zealand (Horak 1973, as "*E. fragile*") and Argentina (Horak 1977, as "*E. fragile*"), differs by a pileus that is initially brown and then turns beige, brown encrusted pigments in the pileipellis hyphae, and abundant clamp connections.

Nolanea tricholomatoidea Karstedt & Capelari, **sp. nov.** FIGS. 2L, 7, 8J,K

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Nolanea tricholomatoidea differs from other *Nolanea* spp by its robust stature, a mostly beige pileus that turns brownish beige at the center; its whitish beige stipe, its often pentagonal basidiospores; its basidial basal clamp connections at the base of the basidia; and the encrusted pigment in the subpellis hyphae.

TYPE—Brazil, São Paulo State, Santo André: Parque Estadual da Cantareira, Núcleo Engordador, 23°20′S 46°41′W, Cachoeira trail, 31.I.2008, F. Karstedt, L.A. Silva Ramos & M. Capelari FK1049 (**Holotype**, SP; GenBank KF771347, KF738939, KF738928).

ETYMOLOGY—the name refers to the tricholomatoid stature.

PILEUS 80–92 mm diam., conico-campanulate or plane, umbonate, pale beige, beige or brownish beige at center, surface smooth or slightly pruinose at center, opaque, hygrophanous, translucent-striate at margin. PILEUS CONTEXT white. LAMELLAE adnexed (almost free), beige, ventricose, subdistant, with 2 tiers of lamellulae. STIPE 100–116 × 8–12 mm, and 39 mm at base, subclavate, beige or whitish, fibrous and fibrillose, with white basal mycelium. ODOR indistinct. SPORE PRINT not recorded.

BASIDIOSPORES 8.7–10 × 7.5–8.7 µm (Q = 1–1.33; Qm = 1.2), isodiametric or subisodiametric, strongly angled, with 5–6 angles in profile view, with an obvious hilar appendix, hyaline or slightly brownish pink, thin-walled. BASIDIA 37–51 × (8.7–)10–15 µm, clavate with a narrow base, hyaline, thin-walled, tetrasporic. LAMELLAE EDGE fertile. PLEUROCYSTIDIA and CHEILOCYSTIDIA absent. LAMELLAR TRAMA regular and hyaline, with hyphae 3.7–17.5 µm diam., cylindrical or slightly inflated, hyaline, thin-walled, septate; subhymenium ramose. PILEITRAMA regular, composed of cylindrical or inflated, hyaline, thin-walled hyphae 3.7–27 µm diam. PILEIPELLIS a cutis, made up of cylindrical, hyaline, thin-walled hyphae 2.5–8.7 µm diam., with rare anticlinal elements; subpellis composed of inflated, hyaline, thin-walled hyphae 16.2–46 × 50–120 µm diam. STIPITIPELLIS a cutis made up of straw-yellow, hyaline, thin-walled hyphae, 3.7–7.5 µm diam. CAULOCYSTIDIA absent. CLAMP CONNECTIONS present in the hymenium. REFRACTIVE HYPHAE present in the pileipellis.

HABITAT—Solitary, on soil.

ADDITIONAL SPECIMEN EXAMINED—**BRAZIL. RIO DE JANEIRO STATE, Nova Iguaçu**: Reserva Biológica de Tinguá, Ouro road, 8 Dec 2004, M.P. Albuquerque & A.A. Carvalho-Jr. 29-VI (RB415680).

COMMENTS—*Nolanea tricholomatoidea* was collected in Rio de Janeiro State but reported as *Entoloma lividoalbum* (Kühner & Romagn.) Kubička

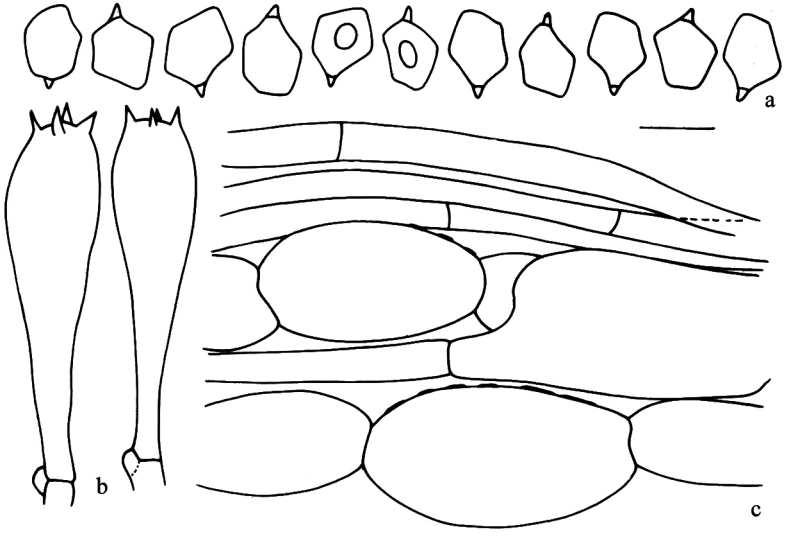

Fig. 7. *Nolanea tricholomatoidea* (holotype, FK1049):
a. Basidiospores; b. Basidia; c. Pileipellis.
Scale bars: a, b = 10 μm, c = 20 μm.

(Albuquerque & al. 2007). The robust stature is reminiscent of a feature common to *Entoloma* sensu stricto, and based mainly on its stature, its umbonate pileus that is sometimes translucent-striate, and its white stipe, *N. tricholomatoidea* might seem related to species of *Entoloma* s.s., such as *E. lividoalbum* and *E. prunuloides* (Fr.) Quél.

Entoloma lividoalbum, described from Europe and recorded from the United States, differs in its pileus that varies from dark brown, dark yellowish brown, pale yellowish white to pale grayish beige, and clamp connections that are present in all tissues (Largent 1994, Noordeloos & Polemis 2008). *Entoloma prunuloides*, recorded from Europe, differs in its smaller basidiospores (6.5–8 × 6.5–8 μm), an ixocutis-type pileipellis, and the presence of clamp connections in all tissues (Noordeloos 1992).

Although a tricholomatoid stature is uncommon in *Nolanea*, the pileipellis structure in *N. tricholomatoidea,* comprising a subpellis with inflated elements and a suprapellis with thin elements, is a feature shared among many *Nolanea* spp.

Discussion

The phylogenetic analyses as supported by ML, MP, and BPP cluster the species described here and other species traditionally accepted as *Nolanea* within a single clade, the /Nolanea clade (Fig. 1).

Four of the species described in this paper—*Nolanea albertinae*, *N. atropapillata*, *N. pallidosalmonea,* and *N. tricholomatoidea*—occur in litter or soil and have heterodiametric basidiospores. They cluster in clade I. *Nolanea parvispora,* the only lignicolous species and characterized by isodiametric basidiospores, clusters in clade II.

Species that are placed in *Nolanea* often have a mycenoid habit (Henkel & al. 2014, Largent 1994, Noordeloos 1992, 2004, Noordeloos & Gates 2012). *Nolanea tricholomatoidea* described herein and the two species classified as *Entoloma* s.s. (*E. pallideradicatum* Hauskn. & Noordel. and *E. valdeumbonatum* Noordel. & Meusers) have a tricholomatoid habit and yet are included in the /Nolanea clade. These species share with *Nolanea* species a pileipellis with a subpellis composed of inflated hyphae and heterodiametric basidiospores.

Curiously, all species studied and almost all species (that have been published with a detailed description of the pileipellis) in the /Nolanea clade have a pileipellis composed of a suprapellis with narrow hyphae and a subpellis with inflated hyphae. We recommend paying careful or close attention to this character in the future to determine if these features are phylogenetically informative.

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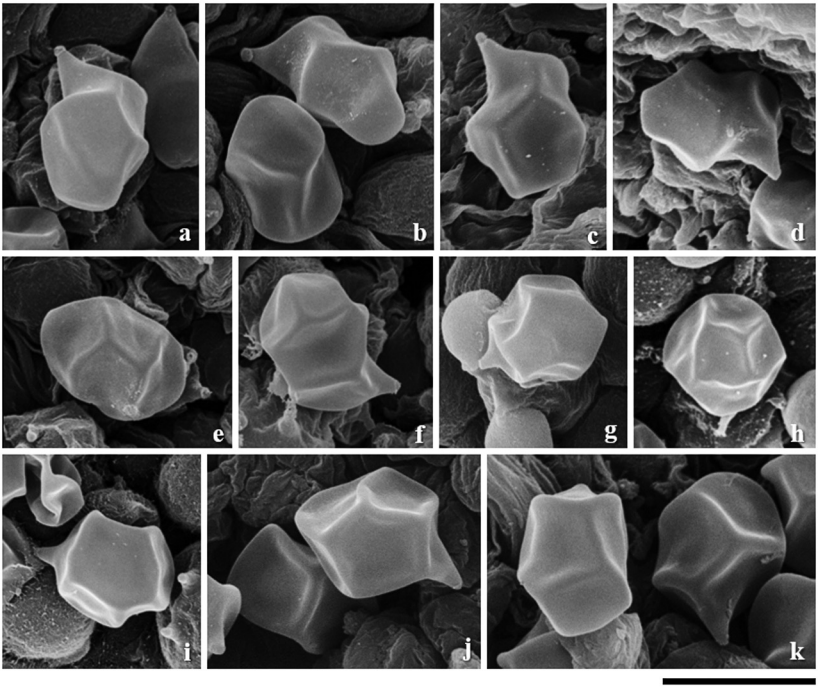

Fig. 8. Basidiospores in SEM:
a, b. *Nolanea albertinae*; c, d. *N. atropapillata*;
e, f. *N. pallidosalmonea*; g–i. *N. parvispora*;
j, k. *N. tricholomatoidea*. Scale bar = 10 µm.

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